Simulating the Effect of Landscape Size and Age Structure on Cavity Tree Density Using a Resampling Technique

Zhaofei Fan, Stephen S. Lee, Stephen R. Shifley, Frank R. Thompson III, and David R. Larsen

ABSTRACT. Cavity-tree density (CTD) is an important indicator of habitat quality for cavity-dependent wildlife. However, the abundance of cavities and cavity trees can vary dramatically, even among trees or stands with similar attributes. This uncertainty can make it difficult to expand stand-level estimates of cavity abundance to large landscapes, although it is often desirable to do so. This limits the utility of CTD as a measure of habitat quality. We use a resampling method (statistical bootstrap) to construct a set of regression models to predict CTD based on landscape age structure and landscape size. The estimated regression coefficients are highly variable (in terms of the adjusted R^2 and root mean square error) for landscapes $<$100 ha, but the models perform well for larger landscapes. We test the regression models using an independent data set from the Missouri Ozark Forest Ecosystem Project (MOFEP) and find that the mean relative error (RE) when predicting CTD for landscapes between 300 and 4,000 ha is less than 10%. Both the size (in hectares) of the landscape and the stand age-class components affect RE; but RE decreases with increasing landscape size in a consistent and quantifiable manner. For Ozark landscapes $\geq$100 ha, knowledge of the proportion of the area in the seedling/sapling, pole, sawtimber, and old-growth age classes can be used to readily estimate the number of cavity trees and how that number will change if the landscape age structure is altered. FOR. SCI. 50(5):603–609.

Key Words: Regression, bootstrap, relative error, Missouri.

CAVITY TREES (EITHER LIVE OR DEAD) are trees with holes or other structures large enough to shelter animals. They are integral components of forest ecosystems and provide habitat for a wide variety of wildlife species (e.g., Conner et al. 1975, Scott et al. 1977, Titus 1983, McClelland and McClelland 1999). At the landscape level, cavity-tree density (CTD) is an important measure of habitat quality. In Missouri, for example, wildlife management guides recommend maintaining 17 cavity trees per hectare to meet the needs of wildlife (Titus 1983).

Formation of cavities begins when a tree or part of a tree dies or is injured by a disturbance event such as fire, insect attack, disease, animal excavation, or mechanical injury (Carey 1983). The spatially stochastic nature of the cavity-formation

Zhaofei Fan and David R. Larsen, School of Natural Resources, Univ. of Missouri, 203 ABNR Bldg., Columbia, MO 65211-7280—Fax: 573-882-1977; fanzha@missouri.edu, larsendr@missouri.edu. Stephen S. Lee, Div. of Statistics, College of Science, Univ. of Idaho, Moscow, ID 83843—stevel@uidaho.edu. Stephen R. Shifley and Frank R. Thompson III, USDA-Forest Service, North Central Res. Sta., 202 ABNR Bldg., Univ. of Missouri, Columbia, MO 65211-7260—sshifley@fs.fed.us, frthompson@fs.fed.us.

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process often causes the abundance of cavities to vary widely among trees and the abundance of cavity trees to vary widely among stands (plots), even when the trees or stands are similar in many other respects (Fan et al. 2003a, 2003b). Moreover, unlike conifer forests where most cavity trees (>90%) are dead (snags), over 80% of cavity trees in Missouri and many central hardwood forests are alive (Goodburn and Lorimer 1998, Fan et al. 2003a). These factors complicate the detection, monitoring, and management of the cavity-tree resource in hardwood forests because cavities in live trees can be difficult to detect, the occurrence of cavities or cavity trees is difficult to accurately predict at the tree and stand level, and live cavity trees are often targets for removal in silvicultural practices.

A comprehensive approach to cavity-tree estimation and management requires consideration of multiple spatial scales, including trees, stands, and landscapes. Tree and stand attributes that are regularly used to guide forest management (e.g., age, species, size structure) are not particularly good predictors of the abundance of cavity trees for small cohorts or individual stands. However, for large populations of similar trees or of similar stands, those attributes have been used effectively to predict mean cavity-tree abundance (e.g., Carey 1983) and probabilities of cavity-tree occurrence and abundance (e.g., Fan et al. 2003a, 2003b). The latter specifically models the variation in cavity abundance.

In concept, cavity-tree abundance on a landscape can be derived by simply summing the observed or estimated number of cavity trees found there. In practice, however, aggregation of information about individual trees is impractical for large landscapes because of the cost of acquiring tree-level data. Stands (or plots) have proven to be a more suitable scale for estimating landscape-level resource characteristics via aggregation (Baskerville 1992). Two components are needed to predict cavity-tree abundance and dynamics on a landscape level: a stand-level (or plot-level) model that estimates the distribution of cavity trees and an algorithm to aggregate predictions to the landscape scale (e.g., linear weighted averaging or stochastic resampling methods). A stand-level cavity-tree model can either predict the mean cavity abundance per stand (e.g., standard regression or a generalized additive model) or define a probability density function describing probabilities of cavity abundance for a range of stand conditions. Because cavity trees are relatively rare (approximately 1–3% of all trees) and highly variable among stands (plots), stand-level models that predict only mean cavity-tree abundance overlook interesting information about variation in the cavity-tree resource and are often imprecise (e.g., Carey 1983).

Fan et al. (2003a, 2003b) used stand-age classes to predict the probability associated with a range of cavity abundance values, thus incorporating the stochastic nature of CTD into the estimate at the stand level. We applied that model to thousands of hypothetical landscapes and nine real landscapes to explore effects of landscape size and age structure on CTD. Specifically, we applied a resampling technique (bootstrap) and used the results to examine how landscape size affects the precision of estimated mean cavity-tree abundance. We (1) simulated the CTD for a wide range of landscape age structures, (2) quantified the effect of the landscape size on the precision of estimates of CTD and on the relationship of CTD to landscape age structure, (3) developed a simplified regression model for large landscapes that is suitable for estimating cavity-tree abundance based solely on landscape area by age class, and (4) tested the regression model with an independent data set. The models can be linked to stand inventories to estimate or monitor cavity-tree abundance for landscapes where the stand ages are known. Moreover, this information can help resource managers and planners forecast the impact of management activities (e.g., those that alter stand ages) on the future cavity resource.

Methods

Landscape-Level Resource Assessment and Monitoring

From a statistical perspective, a landscape is a finite population **U** composed of individual units (patches) U_1, U_2, . . . , U_n differing in a resource of interest y (such as cavity trees). The distribution and quantity of y is expected to be similar within individual units (not necessarily contiguous in space), but to differ among the units. One way to estimate the total or mean of y on **U** is to independently take a random sample from units U_1, U_2, . . . , U_n, and then calculate the weighted mean or total as in a typical stratified sample. Because landscapes constantly change in response to disturbances (e.g., fire, wind, insects, disease, timber harvest), more often than not our interest is in estimating the change in y relative to the change in units U_1, U_2, . . . , U_n. To predict the dynamics of a resource y on a landscape, it is often possible to (1) derive a distribution (e.g., a probability density function) describing resource y over a wide range of stand conditions, (2) use that model to estimate resource levels for landscape units (e.g., stands) at different points in time, and (3) accumulate results for individual units to get landscape estimates over time. This is commonly done in forest yield and structure projection (e.g., Hyink and Moser 1983, Daniels and Burkhart 1988, Borders and Patterson 1990, Ritchie and Hann 1997) using either deterministic methods (e.g., predicting mean values using regression) or stochastic methods (e.g., estimating values by repeated draws from a probability density function). Both methods are compatible if the landscape is large. However, if interest lies not only in the projected mean values but also in the variability of resource y on different landscapes, the stochastic estimation method will be the better choice, and it is the approach used in this study.

Three components are required to estimate the dynamics of CTD stochastically via computer simulation: (1) the landscape age structure (the distribution of patches by age class); (2) the cavity-tree distribution by age classes; and (3) a stochastic method to generate CTD by age classes (e.g., the statistical bootstrap) (Efron 1979, 1982, Efron and Tibshirani 1993).

Landscape Age Structure

The age structure of a forest landscape is defined as the age-class distribution of the patches on the landscape. Because it is often difficult to obtain the actual age for all the patches on a landscape, stand-age classes or size classes are most often used in forest management. Generally, given a forest landscape of size s with n age classes, the landscape age structure can be expressed numerically as

$$\mathbf{w} = (w_1, w_2, \ldots w_n) = (s_1/s, s_2/s, \ldots, s_n/s), \qquad (1)$$

where $\mathbf{w} = (w_1, w_2, \ldots, w_n)$ and $\mathbf{s} = (s_1, s_2, \ldots, s_n)$ are, respectively, the n-dimensional array of weights (i.e., proportions by age class) and class sizes (i.e., hectares) of age classes ($i = 1, 2, \ldots, n$), and $\sum_{i=1}^{n} w_i = 1$, $\sum_{i=1}^{n} s_i = s$.

It has been shown previously (Fan et al. 2003a) that broad age classes can be used to describe cavity-tree abundance by age class. Thus, we classified all stands on a landscape into four age classes: 1–30 years (seedling/sapling), 31–50 years (pole), 51 to 120 years (sawtimber), and >120 years (old-growth remnants). Consequently, the n-dimensional landscape age structure in Equation 1 was simplified to a four-dimensional age-class structure, $\mathbf{w} = (w_1, w_2, w_3, w_4)$.

Forest landscapes may be composed of an infinite variety of stand age structures as a result of their disturbance history. We simulated a wide variety of landscape age structures by generating four (the number of age classes) distinct random numbers x_i ($i = 1, 2, 3, 4$) between zero and one (i.e., uniform pseudorandom number generator) and then calculating a random set of weights w_i ($i = 1, 2, 3, 4$) of each age class as

$$w_i = \frac{x_i}{\sum_{i=1}^{4} x_i} \quad (i = 1, 2, 3, 4). \qquad (2)$$

For this study, we constructed 360,000 sets of weights representing different landscape conditions (18 landscape sizes × 200 age-class combinations × 100 replicates). For landscapes of differing size s (hectares), we calculated the corresponding size (in hectares) of each of the four age classes on the landscape as

$$s_i = s \times w_i \quad (i = 1, 2, 3, 4). \qquad (3)$$

Distribution of Cavity Trees by Stand-Age Classes

At the stand level, the distribution of CTD within each age class was depicted by a three-parameter Weibull function (Bailey and Dell 1973). The model is of the form

$$f(z) = \frac{a}{b}\left(\frac{z-c}{b}\right)^{a-1} \exp\left[-\left(\frac{z-c}{b}\right)^{a}\right], \qquad (4)$$

where $z = 0, 1, \ldots, 15$ represents intervals (classes) of CTD: 0, 0.1–10.0, 10.1–20, ..., 145.1–150.0 trees/ha; and $f(z)$ is the associated probability (Figure 1). Parameter estimates for Equation 4 ($P < 0.0001$ for all parameterizations) were previously derived for the seedling/sapling ($a = 0.6875$, $b = 0.8663$, $c = -0.2832$), pole ($a = 0.8387$, $b = 2.3736$, $c = -0.1407$), sawtimber ($a = 1.4529$, $b = 3.5152$, $c = -2.3568$), and old-growth age classes ($a = 2.228$, $b = 7.1656$, $c = -0.8734$) by Fan et al. (2003a).

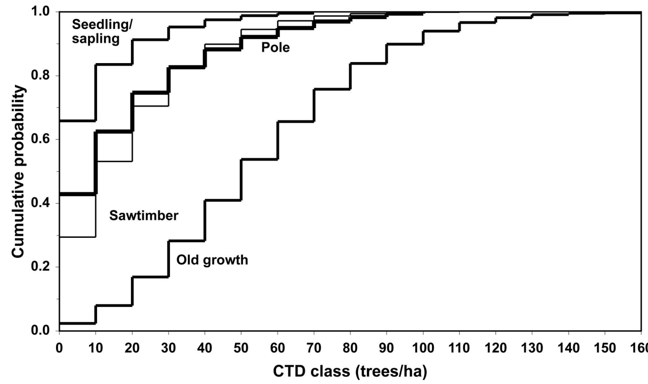

Figure 1. Probability of various densities of cavity trees per hectare by stand size class. Based on Fan et al. (2003a) and Equation 4 using discrete CTD classes.

Estimation of CTD on a Landscape Using the Bootstrap Method

Given a landscape with specified area and age structure defined as weights (Equation 1), for each hectare of the landscape we first randomly drew a CTD interval based on the cumulative Weibull probability (Figure 1) and then randomly drew a specific CTD within the designated interval. We calculated CTD on each landscape as

$$\mathrm{CTD} = \frac{\sum_{i=1}^{4} \sum_{j=1}^{s_i} \mathrm{CTD}_{ij}}{s}. \qquad (5)$$

We repeated this process 200 times for each of 18 different landscape sizes (10, 20, 40, 80, 100, 200, 400, 800, 1,000, 2,000, 4,000, 8,000, 10,000, 20,000, 40,000, 80,000, 100,000 and 1,000,000 ha) to create 200 alternative combinations of weights (w_1, w_2, w_3, and w_4) and CTD (number/ha) for each in the application of the bootstrap method (Efron 1979, 1982, Efron and Tibshirani 1993).

We then combined the CTD estimates for each landscape size and regressed CTD against the weights of three age classes (w_1, w_2, w_3) in a linear model to predict CTD per hectare for a landscape with any given age structure,

$$\mathrm{CTD} = \beta_0 + \beta_1 w_1 + \beta_2 w_2 + \beta_3 w_3 + \epsilon. \qquad (6)$$

Because the sum of the four weights (w_1, w_2, w_3, w_4) always = 1, CTD can be estimated from weights for three of the four size classes with the coefficient for the fourth size class (w_4) included in the constant term, β_0. However, Model 6 can be rewritten

$$\mathrm{CTD} = (\beta_0 + \beta_1)w_1 + (\beta_0 + \beta_2)w_2 + (\beta_0 + \beta_3)w_3 + \beta_0 w_4 + \epsilon, \qquad (7)$$

so the coefficients for each weight explicitly indicate the number of cavity trees per hectare expected in that stand-size class.

Given the variability associated with cavity-tree estimates at the stand (or plot) scale (Table 1), the variability

Table 1. Means and standard errors of the estimated regression coefficients with increasing landscape size for Model 6: CTD = $\beta_0 + \beta_1 w_1 + \beta_2 w_2 + \beta_3 w_3$, where CTD is mean cavity-tree density (trees per hectare) and the weights w_1, w_2, and w_3 refer to the proportion of the landscape in the seedling/sapling, pole, and sawtimber stand age classes, respectively. Coefficients are also applicable with Model 7. Coefficients stabilize and standard errors decrease with increasing landscape size.

Landscape Size (ha)	$\hat{\beta}_0$	$\hat{\beta}_1$	$\hat{\beta}_2$	$\hat{\beta}_3$
	(mean ± SE)			
10	24.0887 ± 3.1940	−29.8616 ± 4.7006	−26.9265 ± 4.3649	−22.1897 ± 4.6341
20	46.4155 ± 1.0304	−49.5992 ± 1.7879	−44.3411 ± 1.6804	−40.7350 ± 1.5569
40	46.3766 ± 0.6555	−45.8921 ± 1.0323	−38.7787 ± 1.1322	−34.8532 ± 0.9344
80	47.8386 ± 0.3097	−44.6237 ± 0.5195	−36.5778 ± 0.5561	−34.7255 ± 0.4995
100	48.2636 ± 0.3219	−44.4470 ± 0.4828	−36.2803 ± 0.4220	−34.9586 ± 0.4469
200	49.0499 ± 0.1933	−43.8214 ± 0.3109	−36.2782 ± 0.3006	−34.8156 ± 0.2933
400	49.4099 ± 0.1125	−43.8730 ± 0.1919	−36.6175 ± 0.1877	−34.4817 ± 0.1765
800	49.2287 ± 0.0597	−43.4503 ± 0.0958	−36.1104 ± 0.0893	−34.0734 ± 0.0783
1,000	49.3286 ± 0.0480	−43.5254 ± 0.0794	−36.2403 ± 0.0740	−34.1347 ± 0.0854
2,000	49.4547 ± 0.0283	−43.6638 ± 0.0495	−36.3601 ± 0.0507	−34.1537 ± 0.0448
4,000	49.4274 ± 0.0211	−43.6150 ± 0.0283	−36.3103 ± 0.0389	−34.0894 ± 0.0313
8,000	49.4635 ± 0.0121	−43.6481 ± 0.0181	−36.3426 ± 0.0209	−34.1192 ± 0.0203
10,000	49.4694 ± 0.0094	−43.6527 ± 0.0164	−36.3459 ± 0.0147	−34.1189 ± 0.0171
20,000	49.4600 ± 0.0059	−43.6348 ± 0.0102	−36.3307 ± 0.0109	−34.1017 ± 0.0099
40,000	49.4599 ± 0.0048	−43.6327 ± 0.0079	−36.3267 ± 0.0081	−34.1001 ± 0.0078
80,000	49.4609 ± 0.0039	−43.6313 ± 0.0051	−36.3275 ± 0.0061	−34.1036 ± 0.0052
100,000	49.4607 ± 0.0030	−43.6307 ± 0.0041	−36.3266 ± 0.0049	−34.1037 ± 0.0040
1,000,000	49.4612 ± 0.0009	−43.6312 ± 0.0015	−36.3271 ± 0.0013	−34.1045 ± 0.0014

associated with the landscape estimate of mean CTD per hectare in the Model 6 will have higher variability for small landscapes than for large landscapes. To evaluate the effect of the landscape size on CTD, we calculated the mean and standard error for the estimated parameters (β_0, β_1, β_2, and β_3) for landscapes of varying sizes by repeating the entire experiment 100 times for each landscape size. This provided robust estimates (mean and standard error) of the coefficients in Model 6 applicable to a wide range of landscape conditions.

Validation of the Fitted Regression Model

We used an independent cavity-tree data set from the Missouri Ozark Forest Ecosystem Project (MOFEP) (Jensen et al. 2002) to examine the accuracy of the landscape-level regression Model 6. MOFEP is a long-term experiment initiated in 1989 by the Missouri Department of Conservation to evaluate the effects of forest management alternatives on multiple ecosystem attributes including cavity trees (Sheriff 2002). In that study, forest conditions and CTD were measured on 648 0.2-ha circular plots across nine sites ranging from 314 to 516 ha (Shifley and Brookshire 2000). We applied Model 6 and computed the relative error (RE) of the CTD estimates for the nine MOFEP sites:

$$\mathrm{RE} = \frac{\text{predicted CTD} - \text{observed CTD}}{\text{observed CTD}}. \tag{8}$$

To assess the landscape size effect, we calculated the RE for larger composite landscapes derived by randomly combining multiple MOFEP sites and regressed RE against landscape size. Because RE is a proportion ranging between −1 and 1, we applied the arc sine square root transformation before regression to stabilize the variance. (Neeter and Wasserman 1974).

Results

When landscape size was ≤20 ha, the regression residuals for Model 6 indicated a negative bias in estimated CTD. For small landscapes, the estimated CTD was highly variable and regression coefficients (Table 1) were imprecise. Some CTD estimates for landscapes ≤20 ha were even negative, providing strong evidence that Model 6 was not suitable for application to such small landscapes. When landscape size was >20 ha, however, neither bias nor nonnormality of the residuals was detected, indicating that Model 6 was pertinent to describing the relationship between CTD and the proportions (w_1, w_2, and w_3), respectively, of the seedling/sapling, pole size, and sawtimber stands on a landscape, given the four stand-age (size) classification system. As expected, the variation inherent in Model 6, in terms of the magnitude of residuals, decreased markedly as the landscape size increased (Figure 2), suggesting that the precision of the estimated CTD increased with increasing landscape size.

The R^2 increased steeply from 0.35 to 0.98 as landscape size increased from 10 to 100 ha, and then reached its plateau (Figure 3). The RMSE changed in an inverse manner. Coincidently, the estimated regression coefficients (β_0, β_1, β_2, and β_3) of Model 6 varied considerably until the landscape size increased to 100 ha (Table 1 and Figure 4). As landscape size increased, the estimated parameters gradually stabilized with small fluctuations around their asymptotic values. When the landscape size was >4,000 ha, the variation in the regression coefficients had no practical significance (Table 1). Based on the R^2 and RMSE changes (Figure 3) and the change of the estimated regression parameters over landscape sizes (Table 1, Figure 4), the minimum landscape size needed to estimate CTD with

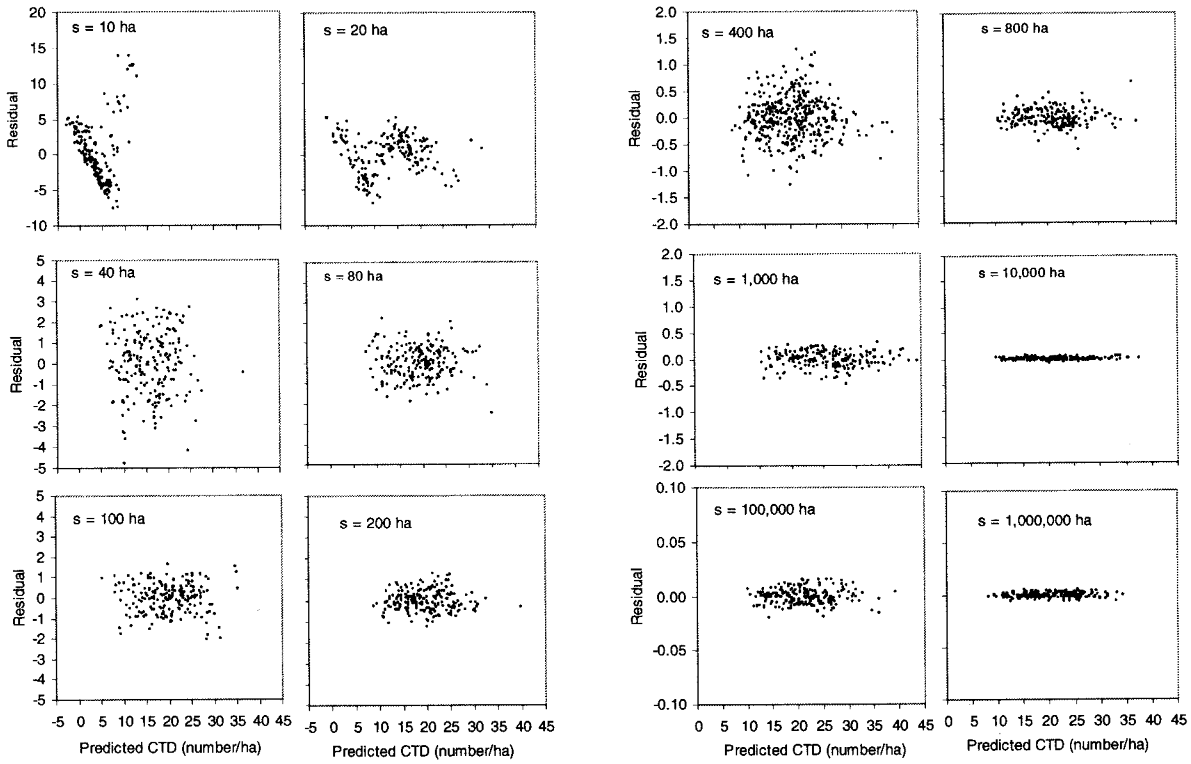

Figure 2. Selected scatter plots of residuals against predicted CTD over landscape size. Note that scales for the *y*-axis differ among graphs and the magnitude of the residuals decreases as landscape size (*s*) increases.

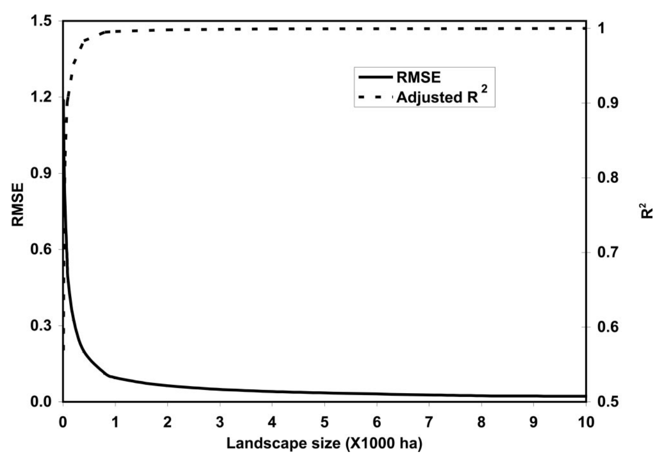

Figure 3. Change of the RMSE and adjusted R^2 for landscapes ranging from 10 to 10,000 ha (*s*). Based on the regression of relative error against landscape size.

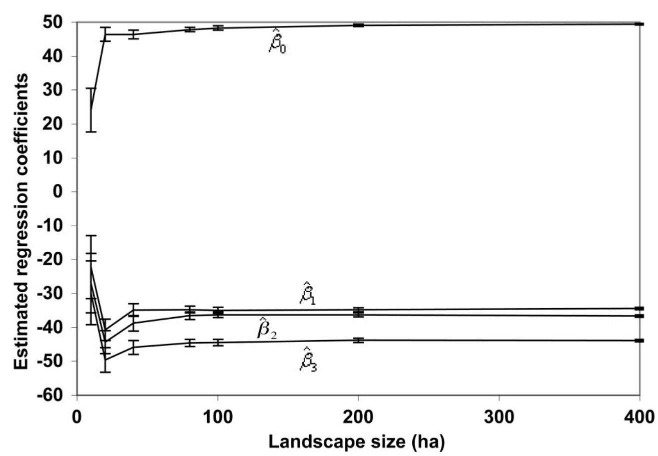

Figure 4. Change of the estimated regression parameters of Model 9 for landscapes ranging from 10 to 400 ha. The vertical bars show the 95% confidence interval of the estimated parameters based on 100 bootstrap replicates.

reasonable precision using Model 6 is 100 ha. To predict the CTD on the landscapes 100–4,000 ha, the appropriate models should be chosen from Table 1 based on the corresponding landscape size. For large landscapes (>4,000 ha), the CTD was estimated as

$$\text{CTD (\#/ha)} = 49.5 - 43.6w_1 - 36.3w_2 - 34.1w_3 \qquad (9)$$

or

$$\text{CTD (\#/ha)} = 5.9w_1 + 13.2w_2 + 15.4w_3 + 49.5w_4. \qquad (10)$$

Equations 9 and 10 are numerically equivalent, but the coefficients in Equation 10 are interpretable as CTD for each age class.

The RE of the predicted CTD based on Model 6 averaged 8% for the nine MOFEP validation sites (314–516 ha), but for sites 6 and 9, the model generated large RE of 29 and −34%, respectively. When these sites were randomly combined to represent larger landscapes, the range of RE values was reduced fourfold and the mean relative error decreased from 15 to 6% (equivalent to the decrease from 0.4 to 0.25 in the transformed RE shown in Figure 5). For the nine combined MOFEP sites (nearly 4,000 ha), the calculated RE

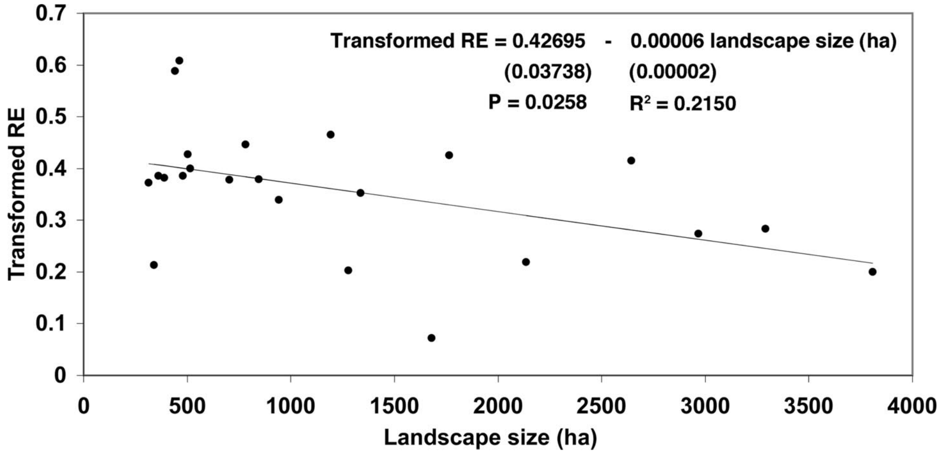

Figure 5. The transformed RE versus landscape size when Model 6 and Table 1 are used to estimate cavity-tree density per hectare for individual MOFEP validation sites and groups of MOFEP sites in combination to form various landscape sizes.

was 4%. The transformed RE was significantly ($P = 0.03$) and negatively correlated with the landscape size.

Discussion

Managers can readily apply Models 6 or 7 with the coefficients in Table 1 to estimate CTD or total cavity abundance for landscapes. The models perform poorly for landscapes smaller than 100 ha. However, for larger landscapes they provide a simple method to estimate cavity abundance based solely on knowledge of landscape area by age class. The age classes used in the model (1–30, 31–50, 51–120, and >120 years) generally correspond to the seedling/sapling, pole, sawtimber, and old-growth size classes in central hardwood forests. These classes are commonly used in timber and wildlife management when more detailed stand-age data are unavailable. Area by size class in a given landscape is readily obtained typically from forest inventory data, photogrametry, remote sensing, or even visual inspection. Application of Models 6 or 7 is far simpler than alternatives such as field inventory of cavities on large landscapes (e.g., Jensen et al. 2002) or applying stand-based models of cavity abundance across each new landscape of interest (e.g., Fan et al. 2003a).

The regression coefficients in Model 10 explicitly reveal the relative contributions of seedling/sapling, pole, sawtimber, and old-growth areas to cavity-tree abundance. Old-growth areas are expected to average 49.5 cavity trees per hectare, more than three times the number found in the sawtimber (15.4/ha), pole (13.2/ha), or seedling/sapling (5.9/ha) age classes. These estimates make it easy for managers to explore the effect of different age-class distributions on mean cavity-tree abundance at the landscape scale as a prelude to detailed, site-specific planning. For example, based on Model 10, the minimum proportion of old-growth area on a large landscape should not be less than 6% to meet a target of 17 cavity trees/ha. Routine cavity inventories tend to overlook cavities (Jensen et al. 2002). Consequently, the CTD values used to build and evaluate these models are considered conservative estimates.

The use of computer simulation permitted the evaluation of a wide range of age-class combinations and landscape sizes. This extended the utility of the limited quantity of cavity-tree data. It would have been impossible to infer the relationship between CTD and landscape-age composition using either experiments or survey methods. The cost and time to obtain a large sample of cavity-tree estimates for multiple landscapes is prohibitive.

Because of the stochastic nature of cavity-tree distribution and the bootstrap data-generating method, the estimated parameters for Model 6 (Table 1) varied significantly ($P \leq 0.01$) when the landscape was less than 100 ha. As landscape size increased, the estimated parameters gradually approached their asymptotic values and fluctuated around these values (Table 1). The model should not be applied to landscapes less than 100 ha. When the landscape size is 100–4,000 ha, the equation coefficients corresponding to the target landscape size (Table 1) should be used to predict CTD. For large landscapes (>4,000 ha), either of the general models, 9 or 10, can be applied.

Test results based on data from nine independent MOFEP sites ranging from 300 to 500 ha (Jensen et al. 2002) showed that Model 6 could over- and underestimate the CTD for an individual site by more than 30%. But for most sites (7 out of 9), the RE ranged from 2 to 17% with a mean RE of 8% for all nine sites. As shown by Figure 5, landscape size is an important factor affecting prediction precision as indicated by the RE values. For the entire nine MOFEP sites (nearly 4,000 ha), the calculated RE was only 4%. Because of lack of replication, we cannot tell whether the small RE is by chance. However, we randomly chose 5, 6, 7, and 8 sites and combined them to form 4 new landscapes ranging from 2,000 to 3,300 ha. The calculated RE for them ranged from 2 to 16%, with a mean of 7%. With large landscapes (>4,000 ha), the precision of Model 6 will be improved as the landscape components increase in size.

Conclusions

The CTD in a landscape is closely related to the stand-age composition (structure) of the landscape and can be estimated by a simple model based on the proportions of the seedling/sapling (0–30 years), pole (31–50 years), sawtimber (51–120 years), and old-growth (>120 years) age classes in the landscape. The model has low precision for landscapes <100 ha, but for larger landscapes the variability of estimated CTD decreases rapidly with increasing landscape size. The model presents a simple technique to analyze cavity-tree abundance and dynamics on a landscape. We calibrated the model for Missouri, but the technique can be applied in other regions.

Tests with independent data sets indicate that the CTD model was significantly affected by the landscape size. For nine independent validation sites (MOFEP sites ranging 300–500 ha), the relative error of CTD prediction averaged 8%, but with two sites it exceeded 30%. Relative error decreased with landscape size, and the composite relative error for the entire MOFEP study landscape (nearly 4,000 ha) was 4%.

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